SOME OBSERVATIONS ON THE DEVELOPMENT OF PERIDERMIUM CEREBRUM

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(with plates 4–6)

The form of *Peridermium Cerebrum* Peck on *Pinus rigida* in the vicinity of Lakehurst, and Toms River, New Jersey, has presented several points of interest. Specimens of this fungus on *P. virginiana* from Bedford, Virginia, have been available for comparison through the kindness of Professor R. A. Harper.

The prevailing type of infection observed in New Jersey appears as circular or elongated canker-like swellings on trunks ranging up to eighteen inches in diameter. Where suckers developed after trees had been cut down, the recent infections appear as globular or fusiform swellings. The canker-like swellings on the trunk are the common form of the fungus. Infections are frequently found at the base of the tree as well as at varying heights on the trunk, usually below the region bearing branches. The trunk infections often consist of a number of closely associated swellings, the outermost being smaller and younger developments. The galls vary in size and are circular or elliptical in outline. This difference in the shape of the swellings suggests that the infection may sometimes progress more rapidly in one direction than in the other. Stewart,* studying the globoid galls of *P. Cerebrum* on *Pinus Banksiana*, is of the opinion that the fungus spreads quite as slowly vertically as it does horizontally. In several cases at Lakehurst protuberant elongated swellings were found developing parallel with the trunk, and were at least six times as long as they were wide. On the other hand, the invasion of the host by the fungus is sometimes more rapid peripherally than it is vertically. The disease in this material obviously

* Stewart, A. Notes on the anatomy of *Peridermium* galls. Am. Jour. Bot. 3: 12–22. 1916.

progresses by the development of secondary ovoid slightly protuberant galls, so that very often at least half of the trunk is girdled. The more central swellings, when they are closely associated, are usually dead. The whole trunk is slightly bent at this point. This bending is due to the inhibition of growth and the death and decay of the region of original infection. The typical condition is that of death at the center and proliferation at the margin. In many cases the entire affected area is dead, owing to the action of such agencies as fire, insects, and birds. Borer and woodpecker injuries in several instances were found to be the cause of the death of the swellings. Weir* has reported that borers and wood-rotting fungi, entering the burls on *Pinus divaricata*, often hasten the decline of the tree.

While the individual swellings or galls may be circular or elliptical in outline, the total or final effect of the parasite on the host sometimes is such as to bring about a fusiform enlargement of the trunk. An example of this type of infection is shown in PLATE 4, FIG. 2, which is from a photograph of a tree at Lakehurst. The infected area is about five feet from the base of the tree. At the widest part of the swelling the trunk is about eighteen inches in diameter and tapers from this region so that the diameter is about four inches less at the limits of the swollen region. Viewed from the side this tree is seen to be bent or "kneed" in the manner shown in PLATE 5, FIG. 1. This figure is from a photograph of another infected tree from the same region. There are at least ten separate swellings on the canker shown in PLATE 4, FIG. 2. These were outlined with ink on the photograph so that their limits may be made out more distinctly in the reproduction. If we assume that the whole canker is the result of one primary infection and that the point of infection is now shown by the presence of the oldest dead gall shown at the center of the picture, we see how the fungus has spread in all directions. There is no bark on this central gall and the exposed wood is dried and cracked. The second gall, just at the right, is somewhat smaller and circular in outline. This gall is also dead. Above the central gall is a large ovoid one that is dead, but not in the advanced stages of decay. At the right and left in this top row of swellings are

* Weir, J. R. Observations on the pathology of the jack pine. U. S. Dept. Agr. Bull. 212: 1–10. 1915.

two living galls, the smaller of which is producing aecidiospores. The larger one at the left was covered with a thick mass of pitch at this time. On the lower parts of the infected region are five or six other galls, the larger one being dead while the others are alive.

The question as to the manner in which the fungus comes to attack new regions is an interesting one in view of the fact that we have these separate galls, all evidently resulting from one primary infection. The spread of the mycelium appears not to be by gradual encroachment but rather by sudden migration induced by the conditions that are to bring about or have already brought on the death of the tissues of the gall. Some light may be thrown on this question by a study of the specimen figured in PLATE 5, FIG. 1, which is a side view of a portion of a tree ten inches in diameter at the cankered region. The marginal gall (at the right in the picture) is alive, but the other two, both furrowed and denuded, are in advanced stages of decay. A cross section of this same specimen is shown in PLATE 6. The tree was plainly infected when it was very young, evidently in the growing region of the stem at a point about two feet from the ground. The wedge-shaped abnormal discolored gall-tissue can be traced to within three or four rings of the center. By splitting the central wedge we find that, further down, the infected area approaches the very center of the tree. The first gall growth has entirely disappeared, owing to decay. The fungus has spread peripherally by a series of sudden localized migrations. At the right (above) the first migration occurred about the tenth year, and about the fourteenth year at the right-center (below). Both migrations resulted in the formation of large, lobed or furrowed galls, the wood of which is now discolored and decayed. Just when the other migrations took place is difficult to determine. At the upper left corner a distortion of the annual ring is evident at about the twenty-sixth year. At the lower left, the wedge-shaped band of solid, dark-colored wood begins with the eighteenth year and spreads out gradually for eight years more before this section shows the beginning of the globoid gall. It has evidently taken nine years for the upper swelling at the left to develop, although the larger amount of the characteristic gall tissue has been formed during the last three years.

Infections sometimes occur at the base of a tree, as shown in PLATE 5, FIG. 2. This infection has spread peripherally very rapidly. The dark area, at the right of the center, is dead, but the bark still adheres. The other lobes of the gall are producing aecidiospores.

The prevailing type of trunk infection on *P. rigida* in the pine barrens of New Jersey is interesting when compared with those observed by Weir (*l. c.*) on *P. divaricata.* He points out that *Peridermium Cerebrum* in dry sandy areas confines itself more generally to the branches, occurring more rarely on the trunk. In the pine barrens the older swellings are very rough in appearance. Several layers of loose scaly bark are usually found adhering. This is the tissue that is sloughed off after the development of spermogonia or aecidia. It adheres most strongly at the margin of the infected areas. The outer younger swellings possess a smooth tan-colored layer of cork tissue.

In cross sections of the trunk the dark wood of infected areas contrasts so markedly with the healthy wood that the time at which infection took place can be determined fairly accurately. In eight trees that were cut where the disease was restricted to the trunk, it was found that infection had occurred when the trees were from one to four years of age. Cross sections of typical globoid galls on *P. virginiana* from Bedford, Virginia, show that infection usually takes place during the first year's growth. Stewart (*l. c.*) has stated that infection on *P. Banksiana* usually, if not always, occurs during the first year's growth of the branch. Where it is possible to trace the annual rings of growth in *P. rigida* through the infected and uninfected regions, it is found that about twice as much wood is formed in the diseased region as in the healthy.

The mycelium is uninucleated and its intercellular development is abundant in the cortex. The hyphae appear to follow the medullary rays in the cortex as well as in the wood where the mycelium is more sparingly developed.

Haustoria are commonly developed in the cells of the medullary rays. They are not exceptionally large and have the usual constriction where the cell wall is penetrated. They are of about the same diameter as the hyphae from which they originate and are sometimes found to be adjacent to the nucleus. Occasionally two or three haustoria are found in the same cell. The cells of the cortex are not attacked by haustoria as frequently as are those of the phloëm and medullary rays. Living hyphae with haustoria are found in wood tissue several years old.

We were not fortunate enough to observe the exudation of spermatia in the New Jersey material. Sections of material showed the presence of spermatiophores bearing spermatia as early as March 25. They form a palisade layer that appears to be spread over indefinite areas of considerable extent like a caeoma type of fructification. This palisade is formed beneath four or more layers of newly developed cork cells. The spermatiophore primordium consists of a compact mass of uninucleated cells of mycelium situated just above the outer row of cortical parenchyma cells. Below this the mycelium is sparingly developed as compared with what we find below the aecidium primordium. The Virginia material was more favorable for the study of the spermatial layer. This material consists of the typical globoid swellings as described by most investigators of *P. Cerebrum*. The galls are fairly smooth in appearance compared with the New Jersey material. The development of the palisade layer of spermatiophores bearing spermatia was first observed in sections of material collected February 9. The primordium develops between the cortex and the cork layer as shown in TEXT-FIGURE 1. The overlying cork layer is smooth in appearance. Specimens were placed in moist chambers and within twenty-four hours exudations of spermatia appeared. The cork becomes irregularly cracked so that the spermatia exude in yellowish droplets. There is no special aperture through the bark for the escape of the spermatia; they ooze out as sticky exudations through cracks naturally formed by the growth of the gall. On removing the overlying cork a yellowish crust-like layer of spermatiophores is exposed.

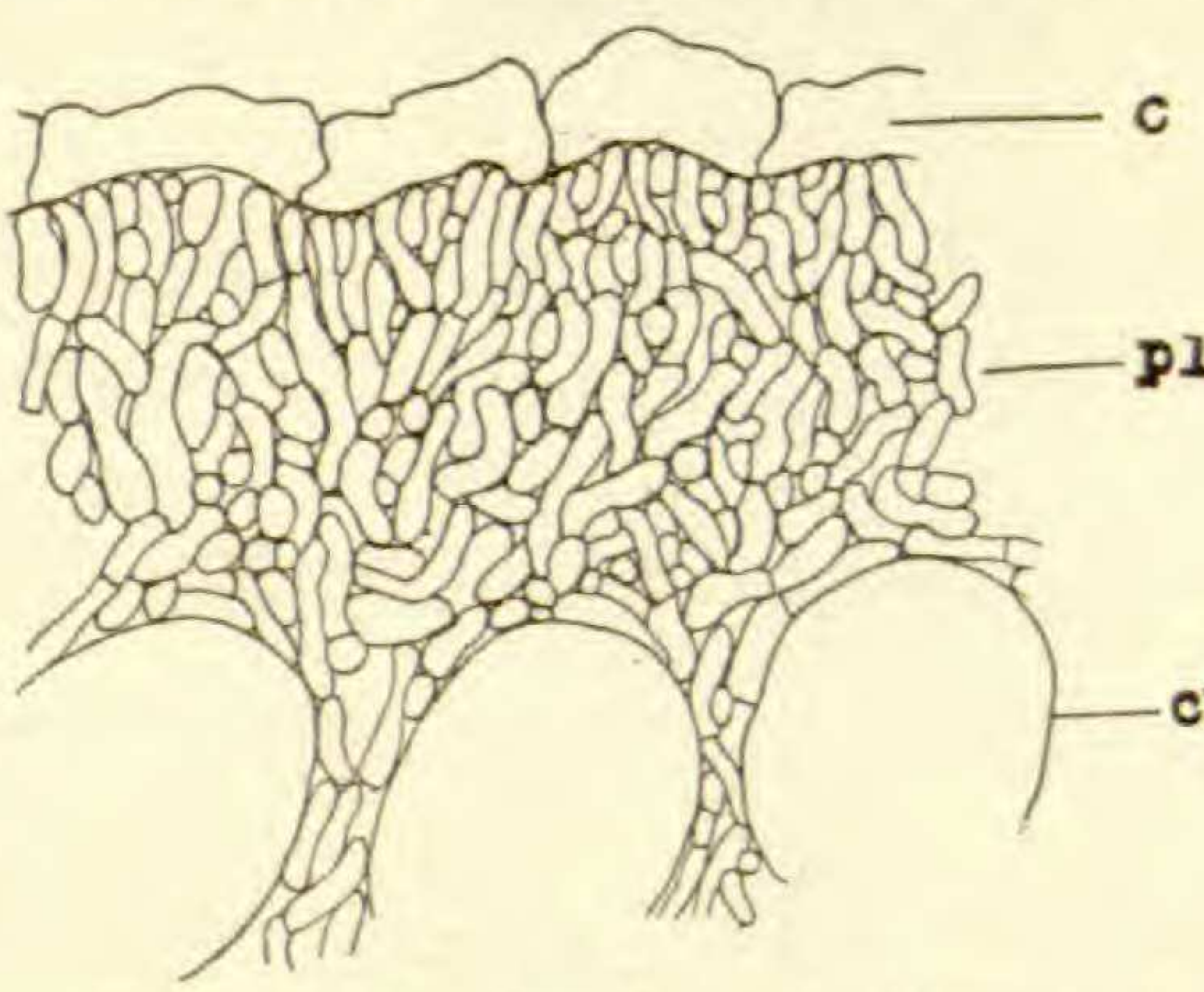


FIG. 1. Section through spermogonial primordium. *c*, cork; *pl*, plectenchyma; *cp*, cortical parenchyma.

This layer is continuous over the gall except where interrupted by small irregular patches or strips of cork that can not be removed easily. A burl with portions of the cork removed is shown in PLATE 4, FIG. 1. The irregular patches of thin cork are outlined to bring out by contrast the smooth, shining spermatiophore surface. A continuous area half an inch square can frequently be uncovered, disclosing the crust-like spermatial surface. Microtome sections three quarters of an inch long have been made, showing a continuous palisade layer. A small portion of a section through a matured spermatial layer is shown in TEXT-FIGURE 2. We have not observed in our sections that this effused palisade of spermatiophores is limited by a definite marginal system of sterile cells. Spermatial primordia frequently extend from the margin of matured areas as a plectenchyma of hyphae between the cork and cortical parenchyma as illustrated in TEXT-FIGURE 1. The cortical cells immediately below the layer of spermatiophores are not spread apart by the hyphae as conspicuously as are those below the aecidium. We have not seen in any instance spermatial hyphae developing in the tissue overlying that in which the aecidia are being formed. Cross sections of the Virginia material developing both spermatial and aecidial fructifications on the same gall show that there is no sharp line of demarcation between the two. In one burl there was a space of only 700 μ separating them. The nature of the spermogonia of *P. Cerebrum*

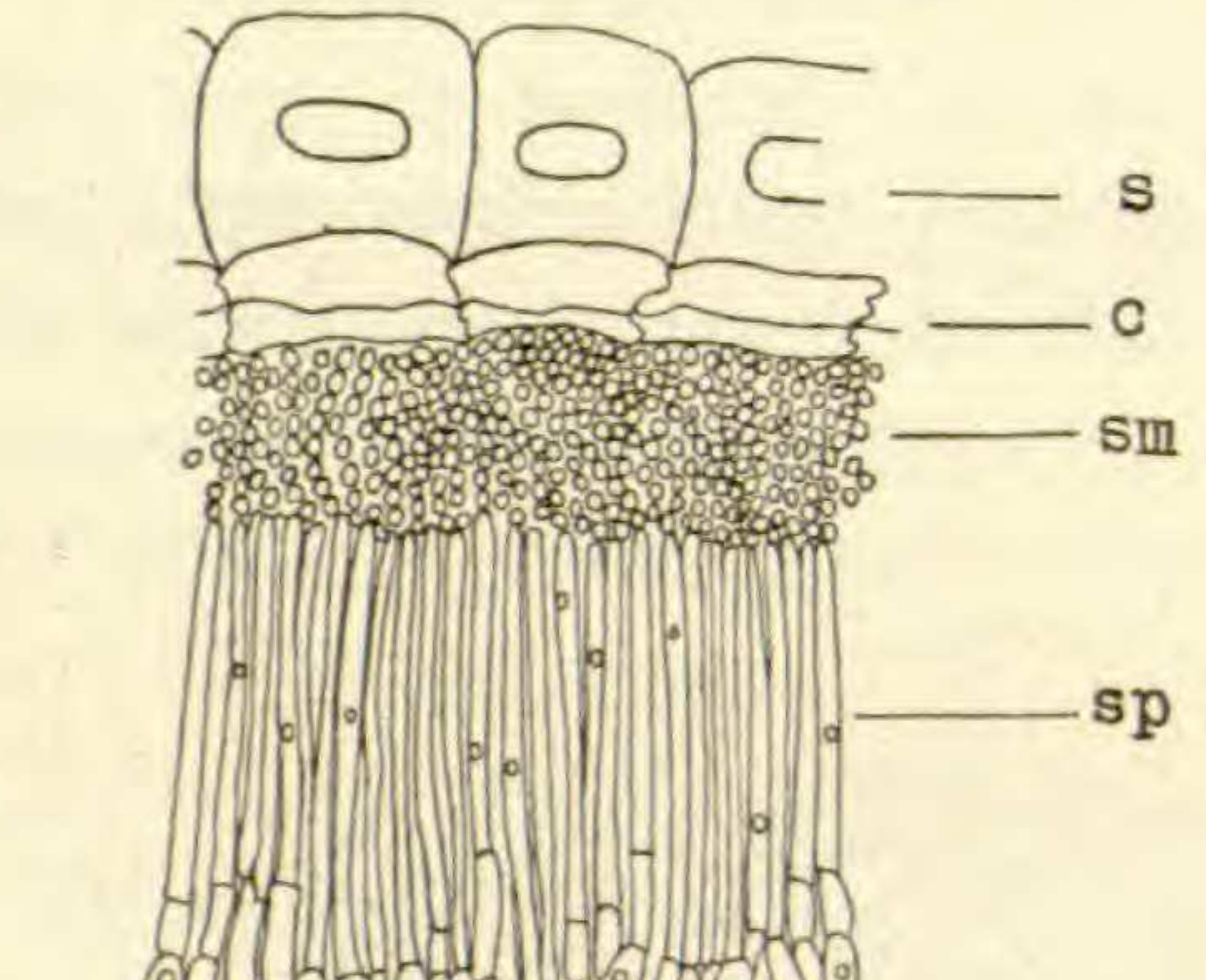


FIG. 2. Section through the cortex showing the spermatial layer. *s*, sclerenchyma; *c*, cork; *sm*, spermatia; *sp*, spermatiophores; *b*, basal tissue; *cp*, cortical parenchyma.

has been noted by Arthur and Kern* and others. We find that the spermogonia are not definitely delimited units. The spermatia are developed from an extensive palisade layer of spermatiophores spreading out indefinitely over the surface of the gall, thus producing a typical caeoma-like structure. Our conception of the meaning of the terms spermogonium and pycnium must be broadened if we are to use either of them in describing this structure.

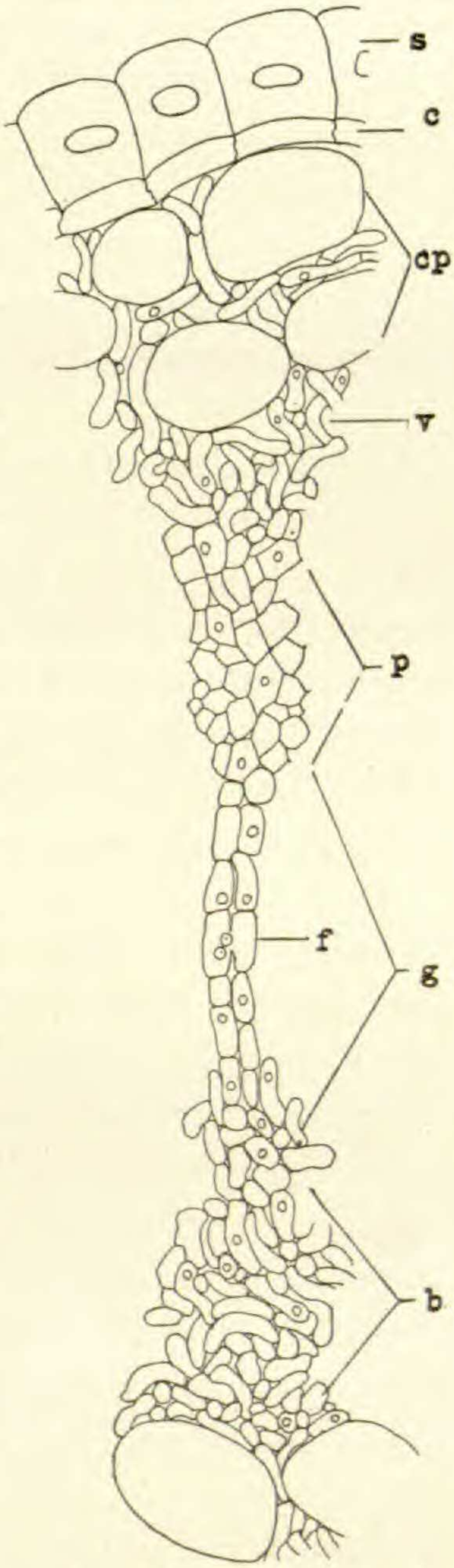


FIG. 3. Section through aecidium primordium from material collected at Bedford, Virginia. *s*, sclerenchyma; *c*, cork; *cp*, cortical parenchyma; *v*, vegetative hyphae; *p*, pseudoparenchyma; *g*, gametophoric hyphae; *f*, fusion cells; *b*, basal tissue.

In the New Jersey material it has not been possible to determine with accuracy very long in advance those swellings which will develop aecidia. The tissue in which aecidia are developed is usually sloughed off by the following spring. It appears as a dry corky layer, the surface of which possesses the cerebroid outline, due to the aecidial scars. The aecidium primordium has been observed in cross sections of material as early as April 29. At this time it appears as an extensive, deep-seated yellowish layer in the cortex, where it can be easily recognized. The cells of the cortex in the region of the primordium are conspicuously separated by the abundant development of the vegetative mycelium. The outer two or three rows of cortical parenchyma cells are pushed outward by the primordium. The relation of the primordium to the host tissue may best be understood by referring to TEXT-FIGURE 3. This figure is drawn from a section of the cortex in

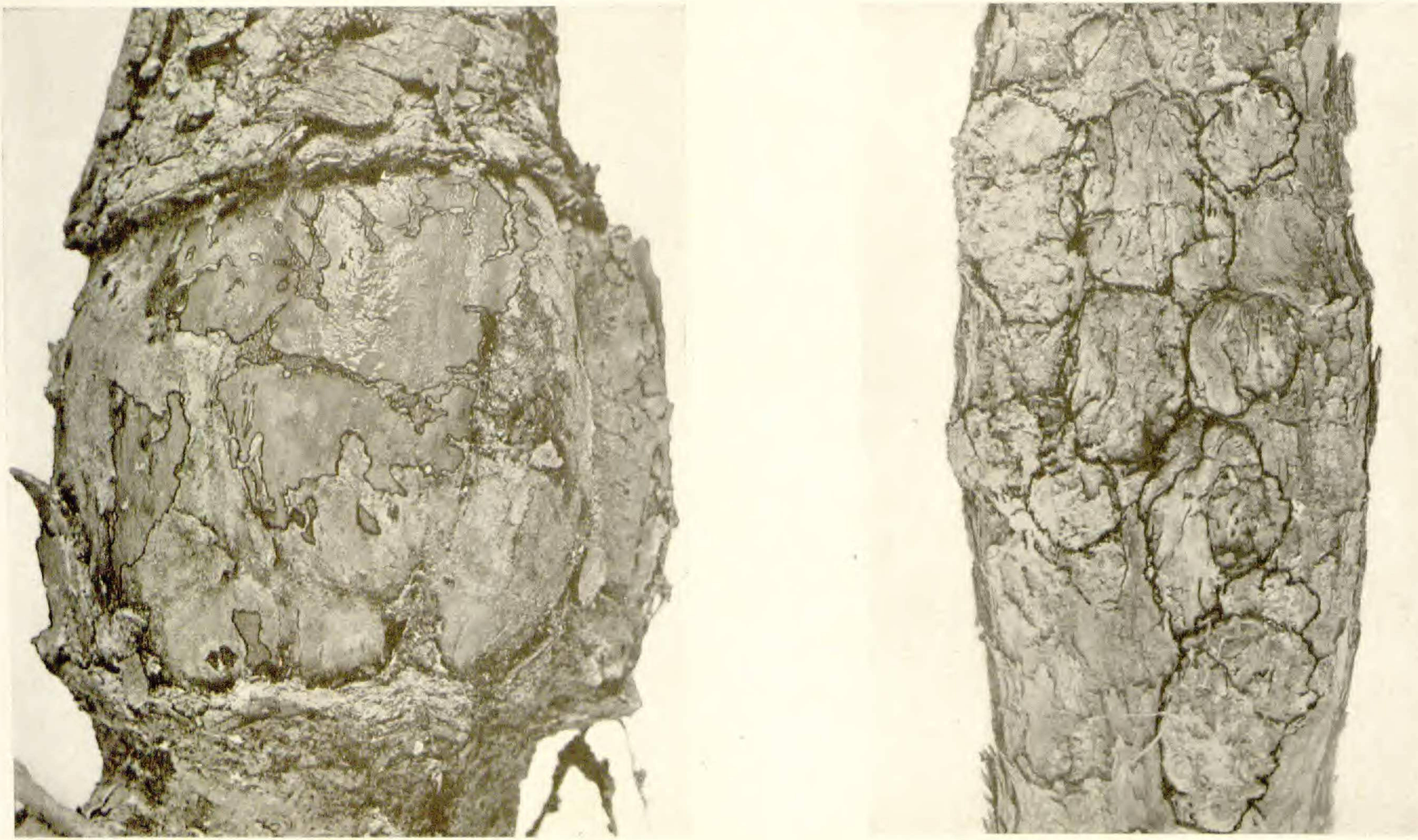
* Arthur, J. C., & Kern, F. D. North American species of *Peridermium* on pine. Mycologia 6: 109–138. 1914.

which the primordium is developed. Only two rows of overlying cortical parenchyma cells are shown in this section. The number, however, varies and there may be as many as four or five layers. Above these outer parenchyma cells (*cp*) there are from one to four layers of flat, thin-walled cells (*c*) and beyond these one to four layers of large sclerenchyma cells (*s*). At the base of the primordium there is a compact mass of interwoven hyphae (*b*) from which parallel rows of cells originate. These are the gametophoric hyphae (*g*) which are eight or more cells in length. The fusion cells (*f*) in these chains are recognized by their being deeply stained in the preparations. Beyond the gametophoric hyphae, in this stage, we find a considerable development of pseudoparenchyma (*p*). Above the pseudoparenchyma the vegetative hyphae (*v*) are shown pushing in between the cells of the outer layers of cortical parenchyma (*cp*). The aecidium has its origin slightly deeper than the spermogonium. In the spring of 1916 at Lakehurst, N. J., the matured aecidia were first observed on May 21.

In no instance have we discovered spermogonia and aecidia following each other on identical areas of the same gall. Certain galls were found developing only aecidia, others only spermatia. In the Virginia material it was found in several instances that both developed on different parts of the same gall. This would indicate there is an alternation of the aecidium and spermogonium as reported by Hedgcock and Long* and others. In the large canker-like swellings of the New Jersey material we have not found galls bearing both aecidiospore and spermatia galls. We have found a few cases of infection on *P. rigida* in New Jersey with the swellings still bearing the rough, scaly bark showing plainly aecidial scars in April. When this was removed we found directly beneath, separated from it by a few layers of new cork, aecidium primordia. This may have been due to the possibility that the old cork layers were not shed the previous year, that is, at the time spermatia were developed.

Seedling oaks of *Quercus ilicifolia* and *Q. marilandica* were found near Lakehurst, New Jersey, with mature uredosori as early

* Hedgcock, G. G., & Long, W. H. Identity of *Peridermium fusiforme* with *Peridermium Cerebrum*. Jour. Agr. Research 2: 247–249. 1914.



PERIDERMIUM CEREBRUM PECK